Early visual responses to upright and inverted faces

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ABSTRACT

OBJECTIVE: The aim of this neuromagnetic study was to investigate neural substrates of face inversion effect at early latencies. METHODS: 306-channel whole-head MEG system was used to record visually evoked responses to centrally presented upright and inverted faces from eight subjects with available MRI scans. MEG responses to four face stimuli were analyzed: upright happy, upright neutral, inverted happy and inverted neutral. Spatio-temporal localization assumed multiple-current dipoles in a spherical volume conductor. RESULTS: Depending on subjects, up to four sources were identified during the first 140 ms after stimulus onset in the occipital, occipito-temporal, and parietal regions. Our preliminary results indicated bigger differences in locations of current dipoles for upright vs. inverted than for happy vs. neutral conditions. CONCLUSIONS: Face inversion effect was evident at early latencies not only by a delayed and decreased amplitude of evoked responses but also by shifts in source locations that were activated by upright and inverted faces, respectively.

KEY WORDS

MEG (magnetoencephalography), face processing, face inversion, facial expression change, multiple-current dipoles, spatio-temporal source localization.

INTRODUCTION

Inversion impairs recognition of faces more than recognition of non-face objects. Behavioral studies suggest that inversion disrupts holistic encoding employed to recognize upright faces [Farah, 1998]. A number of studies have shown delayed first positive deflection in MEG and EEG responses to inverted faces (e.g. [Linkenkaer-Hansen, 1998] [Susac, 2004]). The aim of this study was to examine underlying mechanism of the face inversion effect. Previous study [Watanabe, 2003] with 37-channel magnetometer and a hemi-field stimulation did not find differences in anatomical location of activated regions to upright and inverted faces. In this study we used a whole-head 306-channel system, centrally presented stimuli, and the number of averages was high in order to improve signal-to-noise ratio.

METHODS

Eight men (age 22–40) with normal or corrected-to-normal vision participated in the experiment. All subjects had available MRI scans. The study was approved by an Ethical Committee at the Helsinki University Central Hospital.

Gray-scale face stimuli were presented centrally with a visual angle of 2.7º x 2.2º for 150 ms. During the inter-stimulus interval of 450 ms the subjects fixated on a dark gray cross at the center of the screen. Face stimuli were presented in an oddball paradigm with a task of silent counting of the target face with glasses stimulus. Standard stimuli from four conditions were analyzed here: upright happy (H), upright neutral (N), inverted happy (IH) and inverted neutral (IN) (Figure 1). Eight hundred standard stimuli were presented for each condition.

The MEG data were recorded with a 306-channel whole-head system (Vectorview, Elekta Neuromag, Helsinki, Finland) in a magnetically shielded room (Euroshield Ltd., Eura, Finland) simultaneously with a 60-channel MEG-compatible electrode cap at the BioMag Laboratory, Helsinki University Central Hospital. Horizontal and vertical eye movements were monitored with electro-oculogram (EOG) electrodes placed above and below the left eye and lateral to each eye. Epochs with EOG exceeding 150 μV were excluded from averaging. The data were recorded with a passband of 0.1–200 Hz, sampled at 600 Hz, and averaged on-line. The data were digitally filtered off-line with a 40-Hz lowpass filter. Data analysis was carried out with BESA (MEGIS Software GmbH, Gräfelfing, Germany) and BrainVoyager (Brain Innovation B.V., Maastricht, Netherlands) software packages.

RESULTS

Spatio-temporal localization of current dipoles revealed, depending on subjects, three to four sources activated during the first 140 ms after the stimulus onset in the occipital, occipito-temporal, and parietal regions. Figure 2 illustrates locations and time courses of three dipoles in occipital regions that explained the data for subject S1 in time window 80-140 ms for two conditions. Even visual inspection reveals differences in locations of dipoles through conditions. Table 1 summarizes displacements of sources across all conditions. Displacement was bigger for pairs upright/inverted than for happy/neutral. Source 1 was sensitive to inversion and not to the change of facial expression. Its time course showed that it started slightly later and was weaker for inverted happy face compared to upright happy face (Figure 2).

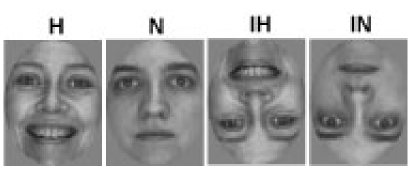

Figure 1. Gray-scale face stimuli: upright happy (H), upright neutral (N), inverted happy (IH) and inverted neutral (IN).

Table 1. Displacement of current sources in millimeters across conditions for subject S1.

	Source 1	Source 2	Source 3
H vs. N	1.6	4.8	12.2
H vs. IH	13.3	7.4	21.2
IH vs. IN	3.2	6.8	9.2
N vs. IN	11.3	15.2	22.4

Locations and dynamics of current dipoles showed inter-individual differences. However, the comparison of displacements across subjects and conditions demonstrated that face inversion for the both facial expressions caused bigger displacement than facial expression change for upright and inverted faces ($p < 0.05$). Time courses of some dipoles (i.e., dipole 1 in Figure 2) showed later activation and smaller amplitudes for inverted faces.

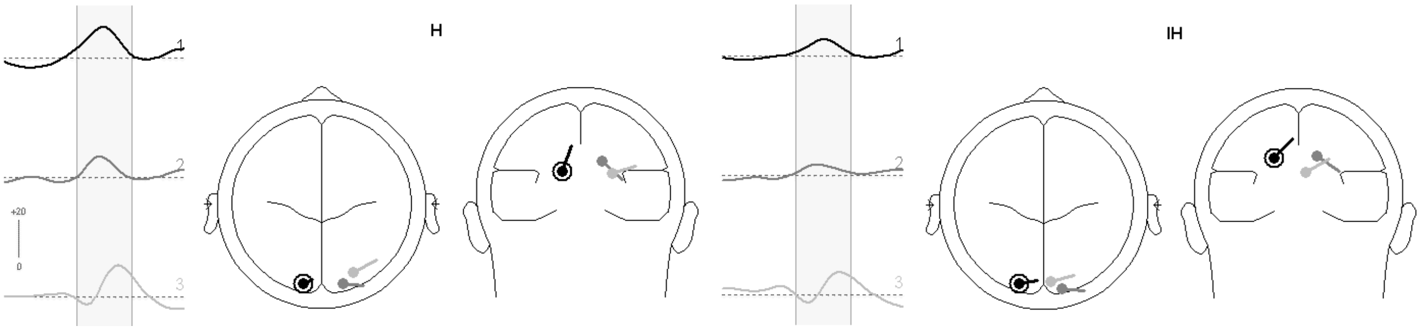

Figure 2. Estimated best-fitting current dipole locations and their time courses in the time window 80-140 ms post-stimulus for subject S1 for upright happy (left panel) and inverted happy faces (right panel). The strength of dipole moments is given in nAm.

DISCUSSION

Previous MEG studies with central presentation of faces reported two ([Linkenkaer-Hansen, 1998]) or one ([Swithenby, 1998]] [Halgren, 2000]) current dipoles or could not determine the location of dipoles before 140 ms ([Sams, 1997]). [Watanabe, 1999] and [Watanabe, 2003] used hemi-field stimulation and identified three sources up to 240 ms. In the present study with centrally presented face stimuli we identified three to four current dipoles during the first 140 ms after the stimulus onset.

In contrast to [Watanabe, 2003] our results demonstrated differences in locations for upright and inverted faces. Such results suggest early processing related to faces because physically the same upright and inverted faces activated distinctive brain regions. [Liu, 2002] reported face-selective MEG response occurring only 100 ms after the stimulus onset. In the present study we found current dipoles active at this latency and their location and dynamics were sensitive to the face inversion. Therefore, our results support Liu's conclusion that initial stage of face categorization takes place as early as 100 ms post-stimulus.

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